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Population Demography for Ecology
Ken Newman

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1.1 Introduction

The word "Demography" is a combination of the ancient Greek words demos, meaning "the people", and "graphy", which refers to the "the writing or recording or study of". One definition of demography is "the science of vital and social statistics, as of births, deaths, diseases, marriages, etc, of populations" (McGraw-Hill, 2005). Our focus here is on ecology and ecological populations, and demography will be defined as the scientific study and characterization of biological populations' structure and dynamics. The simplest structure is total abundance at arbitrary points in time, while more complex structure includes abundances for multiple partitions of a population, e.g., numbers by sex, age, and spatial location. Dynamics refers to changes in structure and abundances over time as well as processes, sometimes called vital rates, which include reproduction, growth, maturity, movement, and mortality, that cause these changes.

People are interested in demography for a variety of reasons. One is inherent curiosity about abundances and dynamics. Why do the numbers of wolves (*Canis lupus*) on Isle Royale (in Lake Superior) fluctuate the way that they do? What effect will decreased snowpack levels have on the geographic range of American pika (*Ochotona princeps*) in Yosemite National Park? Answers to such questions require not only estimates of abundances of the species but also understanding of the factors that affect the abundances and dynamics.

For species harvested commercially, for sport, or for subsistence, e.g., salmon (*Oncorhynchus spp.*), red deer (*Cervus elaphus*), morel mushrooms (*Morchella spp.*), and black duck (*Anas rubripes*), people want to know how harvest affects population abundances and dynamics. Comparison of alternative harvest regulations is facilitated by predictions of the magnitude and sustainability of harvest levels. Predicting the effects of setting harvest regulations, e.g., a bag limit of 10 black ducks for a one month hunting season, requires some understanding of how this mortality might interact with other sources of mortality and other processes, like reproduction or movement. Estimates of the degree to which harvest mortality will be compensatory (removes individuals that would have died anyway from other factors) and additive (the number of animals that will be removed over and above those that would have died from other factors) are useful.

For species declared threatened or endangered by a government agency there are legal mandates for actions to be taken, or avoided, by managers of land or water resources inhabited by the species. Those actions can pertain directly to the population, such as to not take actions that could kill, harm, or harass the species, or indirectly to the species's habitat. To recover the population, interest is in identifying actions to increase the species abundance, e.g., by restoring habitat, and predicting the effects of actions. For example, the United States Fish and Wildlife Service (USFWS) has a mandate to de-

velop "Conservation Management Plans" for species listed as threatened or endangered under the US Endangered Species Act. Such plans must include (a) specification of management actions to conserve the species, (b) measurable criteria which would lead to a determination that the species can be "delisted", no longer declared threatened, and (c) estimates of the time and cost to carry out such actions. Demographic models are central to identifying such actions, to predicting the effects of actions, and to prioritizing multiple actions.

Questions about demographics split into questions about *abundances* and about *processes*. *How many* individuals, or what volume or mass, are there, and were there previously, in the entire population and in subpopulations distinguished by sex, location, age, or genotype? Answering this question is often quite challenging depending on the magnitude of the abundances, geographic location and range, physical size, mobility, degree of elusiveness, and ability to detect individuals. A variety of statistical sampling methods, e.g., mark-recapture, and technological tools and devices, e.g., radio tracking, have been developed to help provide answers to the *how many* question. A variety of methods of estimating population abundances are discussed in Williams et al. (2002), Borchers et al. (2002), Buckland et al. (2001) and Elzinga et al. (2009), with the latter focused on plant populations.

Even if population abundances were known with certainty, questions about population processes remain. Why were the numbers what they were last year and why are they what they are now? What are the relative effects of each process on abundances at specific points in time? For example, how do adult female fecundity rates of salmon, egg hatching success rates, and larval to juvenile survival combine to affect the abundance of juveniles? How do environmental conditions, both natural and anthropogenic, affect these processes?

The focus of this chapter is on mathematical and statistical approaches to answering such *process* questions. Answering these questions involves a population dynamics model (PDM), a quantification of the relationship between past abundance and current abundances. PDMs can characterize how changes in environmental and anthropogenic factors influence population processes, and how changes in these processes translate into changes in population abundances. Measures of the degree of uncertainty as to the consequences are critical as well. For endangered species, PDMs are central to population viability analysis (PVA, Morris et al., 2002). PVAs use PDMs to make predictions about population trajectories, typically via computer simulation. PDMs are used to estimate extinction probabilities as a function of environmental conditions and anthropogenic factors, including accidents, like oil spills, and deliberate actions, like habitat restoration.

Answers to these initial what, why, and how questions often lead to further what, why, and how questions. Answers at the end of sequence of questions can lead to ideas about management actions to take and implementation of a particular action may then be justified by reversing the direction to yield a

so-called results chain (Margoluis et al., 2013). For example, a proposed management action is to plant riparian vegetation along a stream where juvenile salmon rear. The results chain is the vegetation grows and provides increasing shade along the stream, the shade reduces water temperatures, lowered temperatures increases juvenile survival, and population abundance increases. This conceptual understanding guides data collection and long term biological monitoring programs (Reynolds et al., 2016), and further model development. To assess the effects of planting riparian vegetation, a monitoring program collects a time series of measurements of vegetation biomass, hours of shade, stream temperatures, juvenile abundances before and after the month of May (to estimate survival) at both treatment sites and control sites where no planting is done (Before-After-Control-Impact BACI designs, Smith, 2002).

The organization of the remainder of this chapter is the following. Section 1.2 is an overview of components of demography, including subpopulations and processes, while Section 1.3 is a progression of mathematical models more or less corresponding to these components. The next four sections discuss different approaches to modeling population dynamics. Section 1.4 discusses matrix population models (MPMs) which project the abundances of a finite and discrete set of sub-populations forward at discrete points in times. Section 1.5 is on integral projection models (IPMs), which can be viewed as extensions of MPMs where a continuous valued covariate, e.g., length, can be used to characterize sub-populations without arbitrary discretization of the covariate into disjoint intervals. Individual based models (IBMs), discussed in Section 1.6, are the ultimate partitioning of a population into multiple sub-populations where the life history of each individual member of the population is modeled separately. Section 1.7 is on state-space models (SSMs) which are statistical time series models that separate stochastic variation in processes from statistical sampling error in estimates of population components, and can, in principle, contain MPMs, IPMs, and IBMs. Section 1.8 concludes the chapter with pointers to further literature on MPMs, IPMs, IBMs, and SSMs, comments on topics of demography that were minimally or not at all discussed, and thoughts about the future of biological demography.

For convenience some of the more frequently used acronyms are shown in Table 1.1.

1.2 Components of demography

The basic components of demography are abundances and processes. Total abundances at evenly spaced points in time are denoted n_t, t=1,2,...,T. The simplest process is the change in abundance from one time point to the next. Such changes can be expressed either in an absolute sense, $n_t - n_{t-1}$, or a

TABLE 1.1
Listing of frequently used acronyms and their meaning.

Acronym	Meaning
PDM	Population Dynamics Model
MPM	Matrix Projection Model
IPM	Integral Projection Model
IBM	Individual-Based Model
SSM	State-Space Model
PVA	Population Viability Analysis

relative sense, n_t/n_{t-1}, and in both cases we refer to the change as population growth.

If population abundance can be enumerated, then a succinct and completely accurate characterization of the population and its dynamics is trivial. For example, the numbers of fish in an aquarium on July 1, 2011, July 1, 2012, and July 1, 2013 were $n_{2011} = 70$, $n_{2012} = 61$, and $n_{2013} = 82$, respectively. The additive abundance changes were -9 and 21, and the relative changes were 0.87 and 1.34.

Exact enumeration is relatively rare and uninteresting in isolation. Complexity in demographic modeling arises in several ways: (1) multiple subpopulations, (2) multiple processes, (3) environmental and demographic stochasticity, (4) density dependence, (5) competition and predation, (6) human manipulation of process dynamics, (7) uncertainty in abundances.

1.2.1 Multiple subpopulations

Multiple subpopulations are subsets of a populations that are distinguished by attributes, including sex, age, sexual maturity level, spatial location, genotype, and phenotype. Such partitioned populations are sometimes called structured population, e.g., age-structured or stage-structured populations, and, in the case of spatially distinct populations, metapopulations (Levins, 1969).

Partitioning can be subjective and arbitrary, and depends on the available data. Arbitrariness occurs when the distinguishing attributes are continuous variables, such as measures of individual size like weight, height, length. For example, if the variable is weight, the number of partitions can vary as can the labeling of the partitions; e.g., small $= <$ 10 kg, 10 $\leq$ medium $<$ 20kg, and large $\geq$ 20kg. The partitioning of continuous attributes is an important distinction between MPMs (Section 1.4) and IPMs (Section 1.5).

The finest partitioning of a population is at the individual entity level as the values of each individual's characteristics throughout its entire existence are the most complete description possible. This may be conceptually possi-

ble, but usually not practically possible. As a mathematical exercise, however, the modeling of individuals in a population can be useful for elucidating population level dynamics and will be discussed in Section 1.6 on IBMs.

1.2.2 Multiple processes

The process of population growth can be partitioned into multiple processes that include at least survival and reproduction, but can also include movement, individual growth, and maturation. Partitioning a population into multiple subpopulations can lead to additional process partitioning, e.g., age class specific survival probabilities. Partitioning by sex and size affects handling of reproduction, while spatial partitioning requires a movement process and location-specific movement probabilities.

Conversely, the temporal nature of processes, sequential, overlapping, or simultaneous, can lead to population partitioning. For example, a sequence of life cycle processes for salmon is egg fertilization in freshwater, egg hatching and larval emergence, survival to fry stage, smoltification, migration to the ocean, survival in the ocean, migration back to the freshwater, spawning, and death. Subpopulations of a cohort are then distinguished by life stage.

If size is a distinguishing characteristic, defined ordinally (e.g., small, medium, and large) or continuously (e.g., length in cm), then individual growth is a process affecting dynamics. Individual growth dynamics are quantified in terms of the probability of moving from one size class to another (as in MPMs, section 1.4) or by a conditional probability density function for size z'_{t+1} given previous size z_t (as in IPMs, section 1.5).

1.2.3 Stochasticity

Population dynamics are complicated by environmental and demographic stochasticity. Environmental stochasticity is between year (or any time period) variation in underlying vital rates, such as survival or reproduction, that is typically due to variation in environmental conditions such as air temperature or precipitation. Demographic stochasticity is between-individual variability conditional on a specific vital rate; e.g., if the survival probability for 100 fish is 0.7, the number surviving will not be exactly 70 and variation in that number is due to demographic stochasticity. Unless population numbers are relatively low, as for a severely endangered species, demographic stochasticity has little effect on population dynamics compared to environmental stochasticity. A rule of thumb when doing PVA, (Morris et al., 2002) is that demographic variation can be ignored in the case of a single population with at least 100 individuals, and in the case of multiple subpopulations, or life stages, there are at least 20 individuals in the most important subpopulations.

1.2.4 Density dependence

As any population increases in abundance, resource limits necessarily reduce population growth; e.g., values of $n_t/n_{t-1} > 1$ cannot be sustained. Resource limits directly affect survival and reproduction, and influence growth and movement processes, as well, in other words, these vital rates are abundance or density dependent. While decreasing abundance or density typically leads to increases in survival and reproduction, there are situations where decreases in abundance beyond a threshold lower vital rates; e.g., individuals have difficulty finding mates and cannot reproduce, what is known as an Allee effect, a problem for critically endangered species.

1.2.5 Competitors, predators, and prey

Vital rate processes for a given species, say species A, can be affected by the abundance of other species in several ways. If another species, species B, uses the same resources, e.g., consumes the same prey items, the the species are in competition, and the increased abundance of the competitor B lowers the survival and reproduction of species A. If a third species, species C, preys upon species A, then the abundance of the predator C obviously affects survival of A. If a fourth species, species D, is a prey item, then its abundance can also affect the vital rates of A. An important consideration in mathematical modeling is whether abundances of competitors, predators, or prey are treated as covariates, i.e., input variables for vital rates of a given species, or the abundances of these other species are modeled simultaneously in a multi-species PDM.

1.2.6 Human manipulation of dynamics

Human activities affecting population dynamics include harvest and species protection. Survival probabilities in PDMs need to modified by harvest, and reproduction and movement can also be affected. PDMs can be used to evaluate alternative harvest regulations including cases of selective harvest of subpopulations; e.g., only mature male red deer can be harvested during a summer time period. For endangered populations, dynamics are manipulated by regulating human activities and carrying out actions to increase and improve habitat. Projections of the effects of such regulations and actions on population dynamics are central to PVA.

1.2.7 Uncertainty in abundances

Uncertainties about abundance, or vital rates, introduce uncertainty in PDMs over and above the environmental and demographic stochasticity, what (Nichols et al., 1995) label "partial observability". The time at which samples are taken can also affect the ability to estimate various process parameters,

and can affect mathematical model formulation. Rees et al. (2014) give an example of a sequence of processes: reproduction, followed by mortality, and then growth. If abundance estimates are made just before reproduction, abundance change includes a term for the probability of the previous year's reproduction (recruits) living an entire year. If abundance estimates are made just after reproduction, the annual abundance change does not reflect the survival of this year's reproduction as the estimates were made before subsequent mortality, and the survival of the previous year's reproduction is entangled with the survival of the previous year's abundance of old entities (non-recruits). Inserting additional sampling or estimation points in the year is one means of disentangling the effects of multiple processes.

1.3 General mathematical features of PDMs

Here we present various mathematical and probabilistic formulations of demographic models paralleling some of the features of Section 1.2. The simplest demographic model is for a single population with a single deterministic and density independent process. Such a model can be expressed in terms of absolute or relative changes in abundance. Absolute changes, $n_t - n_{t-1}$, translate into additive models,

$$n_t = n_{t-1} + \Delta_t, \tag{1.1}$$

with $\Delta_t < 0$ and $\Delta_t > 0$ indicating decline and growth, respectively, while relative changes, n_t/n_{t-1}, translate into multiplicative models,

$$n_t = \lambda_t n_{t-1}, \tag{1.2}$$

with $0 \leq \lambda_t < 1$ or $\lambda_t > 1$ for decline or growth.

1.3.1 Multiple subpopulations

Partitioning a single population into two or more populations extends the scalar n_t to a vector $\mathbf{n}_t$. For example, if a population of deer is distinguished by three life stages, young, immature, and mature, then the abundance vector at time t is

$$\mathbf{n}_t = \begin{bmatrix} n_{y,t} \\ n_{i,t} \\ n_{m,t} \end{bmatrix}$$

The length of the abundance vector over time need not remain fixed. The effects of a sequence of processes may cause the vector to expand, e.g., following reproduction, or to shrink, following an aggregation of age classes (Buckland et al., 2007).

1.3.2 Multiple processes

Survival and reproduction.

With the additive single population model (1.1), Δ_t can be partitioned into survival and reproduction components,

$$n_t = n_{t-1} + R_t - M_t \tag{1.3}$$

where R_t is the number of (surviving) young produced between $t-1$ and t and M_t is the number of mortalities from the n_{t-1}. R_t and M_t may or may not be functions of n_{t-1}. In contrast, multiplicative models make explicit the dependence of change on previous abundance. Assume that in the interval $(t-1, t)$ mortality occurs first (the fraction surviving begin ϕ_t), followed by reproduction (with rate ρ_t), and there is no additional mortality before time t. Then the growth rate, λ_t (1.2), is simply the product of survival and reproduction:

$$n_t = (1+\rho_t)\phi_t n_{t-1}. \tag{1.4}$$

The order of processes, mortality and reproduction, relative to the time of measurement (t) does not affect λ_t in this case but the following cases demonstrate when order does matter.

A more complex model with subpopulations of young and mature individuals has different survival fractions for just born young and the mature individuals, $\phi_{y,t}$ and $\phi_{m,t}$, and the time t at which abundances are counted relative to the reproductive process affects model formulation. For one scenario, t occurs immediately after reproduction, the young subpopulation are those just born (denoted $n_{0,t}$ in Scenario 1 below). Under a second scenario, t occurs just before reproduction, and, assuming the time interval is one year, the young will be nearly age 1 at the time of counting (denoted $n_{1,t}$ in Scenario 2).

Scenario 1: t just after reproduction
$$\begin{bmatrix} n_{m,t} = \phi_{m,t} n_{t-1} + \phi_{y,t} n_{0,t-1} \\ n_{0,t} = \rho_t(\phi_{m,t} n_{t-1} + \phi_{y,t} n_{0,t-1}) \end{bmatrix}$$

Scenario 2: t just before reproduction
$$\begin{bmatrix} n_{m,t} = \phi_{m,t} n_{t-1} \\ n_{1,t} = \phi_{y,t}\rho_t n_{t-1} \end{bmatrix}$$

Immigration and emigration.

The scalar additive model with reproduction and survival (1.3) can be extended to include immigration and emigration,

$$n_t = n_{t-1} + R_t - M_t + I_t - E_t$$

where I_t is the number immigrating into the population and E_t is the number emigrating from the population. The scalar multiplicative model (1.4) can be extended but does not necessarily remain multiplicative. The ordering of

processes is again important. Assuming that immigrants arrive, and emigrants leave after mortality occurs, but prior to reproduction, the model is

$$n_t = (1+\rho_t)(\zeta_t\phi_t n_{t-1} + I_t)$$

where ζ_t is the fraction of the survivors from n_{t-1} that stay and I_t is again the number of immigrants. If the order of processes change, the model changes. For example, suppose that immigrants arrive and emigrants leave after mortality and reproduction, then

$$n_t = \zeta_t\rho_t\phi_t n_{t-1} + I_t.$$

Movement.

For spatially-defined subpopulations, the process of movement is relevant. Immigration and emigration is of course a movement process but where the individuals are coming from or going to are not distinguished. A multiplicative formulation is more natural than an additive model, and a movement transition matrix can be inserted into the dynamics equation, say $\mathbf{n}_t = M_t\mathbf{n}_{t-1}$ where survival and reproduction are ignored. For example with three regions labeled A, B, and C, a time invariant transition matrix has the following structure.

$$M = \begin{bmatrix} \mu_{A\to A} & \mu_{A\to B} & \mu_{A\to C} \\ \mu_{B\to A} & \mu_{B\to B} & \mu_{B\to C} \\ \mu_{C\to A} & \mu_{C\to B} & \mu_{C\to C} \end{bmatrix}$$

where $\mu_{i\to j}$ is the probability of moving from area i to area j in one time step, and the rows sum to 1.

Individual animal growth.

For subpopulations distinguished by size classes, transition between classes can be modeled as the fractions moving from one class to another. The process is analogous to that for movement between spatial regions. For populations partitioned to the individual entity level, growth from the size, e.g., length or weight, at time t, z_t, to another size at time $t+1$, z_{t+1}, can be modeled by the addition of an individual growth increment, x_{t+1},

$$z_{t+1}|z_t = z_t + x_{t+1}$$

x_{t+1} could be a function of the size at time t, z_t. Such fine scale handling of growth is central to IPMs (Section 1.5) and can be a part of IBMs (Section 1.6).

1.3.3 Stochasticity

The mathematical distinction between demographic and environmental stochasticity is demonstrated using the scalar multiplicative model (1.2). De-

mographic stochasticity arises when, for a given year t, there is constant underlying annual population growth rate, denoted λ, but there is between-individual variation in the growth rate contribution. Environmental stochasticity reflects between year variation in that underlying rate λ_t. Environmental and demographic variation typically coincide, and a hierarchical model makes clear the relationships:

$$\begin{array}{rl} \text{Environmental stochasticity} & \lambda_t \sim \text{Gamma}(\alpha, \beta) \\ \text{Demographic stochasticity} & n_t | n_{t-1}, \lambda_t \sim \text{Poisson}(n_{t-1}\lambda_t) \end{array}$$

Asymptotic results for environmentally stochastic growth rates.

The long term, or asymptotic, behavior of a single population trajectory with environmentally stochastic annual growth rates is tractable and has similarities with deterministic exponential growth models. Consider the following single population model with environmental stochasticity only (ignoring the issue of abundances necessarily being discrete values):

$$n_t \quad = \quad \lambda_t n_{t-1}, \text{ where } \lambda_t \overset{iid}{\sim} \text{Distribution}(\mu, \sigma^2) \tag{1.5}$$

where $E[\lambda_t]{=}\mu$ and $V[\lambda_t]{=}\sigma^2$. Given an initial abundance $n_0 > 0$, n_t can be rewritten as

$$n_t \quad = \quad n_0 \prod_{i=1}^{t} \lambda_i$$

Taking the natural logarithm of both sides of the equation,

$$\ln(n_t) \quad = \quad \ln(n_0) + \sum_{i=1}^{t} \ln(\lambda_i),$$

which can be re-expressed as

$$\frac{\ln(n_t) - \ln(n_0)}{t} \quad = \quad \frac{1}{t} \sum_{i=1}^{t} \ln(\lambda_i) \tag{1.6}$$

The righthand side of (1.6) is the mean of a sequence of independent random variables, $\ln(\lambda_i), i = 1, \ldots, t$. Adding the assumption that the $E(\ln(\lambda_t)^2) < \infty$, the strong law of large numbers says that the average converges to $E[\ln(\lambda)]$. Further, by the Central Limit Theorem, the asymptotic distribution the mean of the log of the "annual" growth rates is normal. Denoting the sample average log growth rate by $\overline{\ln(\lambda))}$

$$\overline{\ln(\lambda))} = \frac{1}{t} \sum_{i=1}^{t} \ln(\lambda_i) \quad \sim \quad \text{Asymptotic Normal}\left(E[\ln(\lambda)], V(\ln(\lambda))\right)$$

Another way to express this result, using the lefthand side of (1.6),

$$\ln(n_t) \quad \sim \quad \text{Asymptotic Normal}\left(\ln(n_0) + tE[\ln(\lambda)], tV(\ln(\lambda))\right)$$

or

$$n_t \quad \sim \quad \text{Asymptotic Lognormal}\left(n_0 \exp(tE[\ln(\lambda)]), tV(\ln(\lambda))\right) \qquad (1.7)$$

Thus, the median population abundance at t is identical to a deterministic exponential growth model.

Stochasticity in individual processes.

Survival, reproduction, movement, individual animal growth, and other processes can be made stochastic. An example is a survival process for a scalar population with a logit-normal model for environmental stochasticity and a binomial distribution for demographic stochasticity. Letting $\phi_{c,t}$ be the survival probability for subpopulation c at time t,

$$\begin{aligned} logit(\phi_{c,t}) &\sim \text{Normal}\left(\beta_{0,\phi,c}, \sigma^2_{\phi,c}\right) \\ n_{c,t} &\sim \text{Binomial}\left(n_{c,t-1}, \phi_c\right) \end{aligned}$$

where $logit(x) = \ln(x/(1-x))$.

1.3.4 Density dependence

In the ecological literature, there are several well-known single population, deterministic and discrete time-indexed models with density dependent population growth rates including the Gompertz (Dennis et al., 2006), Ricker, Beverton-Holt, and logistic models (Gurney and Nisbet, 1998). Here we just present a deterministic Ricker model formulation (taken from Gurney and Nisbet, 1998). The Ricker model originated with fish populations, but is now applied many other kinds of populations.

$$\text{Ricker model} \quad : \quad n_t = (\phi_a + \phi_y b \exp(-cn_{t-1}))n_{t-1}, \quad b > 0, c > 0, \qquad (1.8)$$

where n_t can be viewed as the sum of surviving adults from the previous year ($\phi_a n_{t-1}$) and surviving progeny, with ϕ_y the survival fraction for offspring produced at rate $b\exp(-cn_{t-1})$. The parameter b is the maximum number of offspring per adult, theoretically possible in the absence of any resource limitations, while $\exp(-cn_{t-1})$ is a density dependent dampening of that maximum.

In the case of multiple subpopulations, if the vital rates and abundances for one subpopulation do not affect another subpopulation, then the above univariate density dependent models can be applied on a per subpopulation basis. If subpopulations occupy the same geographic area and compete for resources, then density dependent formulations will include the abundances of other subpopulations. Density dependent dynamics also arise for populations

of different species that are either in predator-prey relationships or competing for an in-common resource.

In the case of multiple processes, e.g., survival, reproduction, movement, and individual animal growth, process-specific density dependence relationships can arise. In the Ricker model, for example, reproduction is density dependent while survival is density independent. Density dependence in movement processes for spatially distinct subpopulations (metapopulations) is likely as the probability of movement from one region to another could be a function of the relative densities of individuals in each region, e.g., the probability of moving from a high density region to a low density region increases as the difference in densities increases. Of course, stochasticity can be incorporated into density dependent formulations for different processes.

Density dependence both within a single population and for populations of two or more different species, e.g., predator and prey populations, can lead to relatively complex population dynamics. The Lotka-Volterra predator-prey model (Gurney and Nisbet, 1998) can with certain parameter combinations lead to periodic oscillations in the abundances of each population. Within a single population, discrete time single population models like the Ricker and discrete logistic model can lead to damped or expanding oscillations, different periodicities, or chaos (no periodicity and apparently random fluctuations; (see, for example, Figure 2.6 in Gurney and Nisbet, 1998).

1.3.5 Inclusion of covariates

Mathematical formulations of population processes often include covariates, one of the earliest examples being the modeling of survival as a function of weather data (North and Morgan, 1979). The effects of deliberate human manipulations or incidental anthropogenic consequences, e.g., the erection of a wind turbine and subsequent bird mortality, can be translated into covariates for process models. Abundances of predators, competitors, or prey can also be used as covariates in models for survival and reproduction of a single species population dynamics model in contrast to jointly modeling the population dynamics of several species. The legitimacy of such handling of these other populations may depend upon the degree to which other populations are affected by the abundance of the population of interest.

1.3.6 Remarks: Estimability and Data Collection.

It is easy to formulate a population dynamics model where the parameters cannot be estimated given the available data. For example, annual surveys alone do not allow separate estimation of the survival probability, ϕ_t, and reproductive rate, γ_t, in the simple univariate model (1.4). Intuitively given estimates of n_t and n_{t-1} one can just estimate the combination $(1 + \gamma_t)\phi_t$.

One way to disentangle such combinations of parameters, in the case of sequential processes, is to have abundance estimates at time points immediately

after the end each process. For example, in the model (1.4) abundance should be measured twice a year, once immediately following the survival process, and once after reproduction. The reality of the processes is typically more complicated, with such sharp demarcations unlikely, but formulating such models can provide guidance for data collection.

1.4 Matrix Projection Models, MPMs

One of the oldest and most popular types of population dynamics models are matrix projection models (MPMs). Lewis (1942) and Leslie (1945) independently proposed MPMs as a means of modeling the population dynamics of age-structured populations (age-specific subpopulations). Let $n_{0,t}$ denote the number of young at time t and $n_{a,t}$ be the abundance for ages 1 to $A-1$, and $n_{A+,t}$ be the abundance of age A and older individuals. A deterministic formulation for the dynamics can be written as

$$\begin{bmatrix} n_{0,t} \\ n_{1,t} \\ n_{2,t} \\ \vdots \\ n_{A,t} \\ n_{A+,t} \end{bmatrix} = \begin{bmatrix} \gamma_0 & \gamma_1 & \gamma_2 & \cdots & \gamma_{A-1} & \gamma_A \\ \phi_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & \phi_2 & 0 & \dots & 0 & 0 \\ \vdots & & & & & \\ \vdots & 0 & 0 & \dots & \phi_A & \phi_{A+} \end{bmatrix} \begin{bmatrix} n_{0,t-1} \\ n_{1,t-1} \\ n_{2,t-1} \\ \vdots \\ n_{A,t-1} \\ n_{A+,t-1} \end{bmatrix} \tag{1.9}$$

or more compactly as $\mathbf{n}_t = \mathbf{L}\mathbf{n}_{t-1}$, where $\mathbf{L}$ is referred to as a Leslie matrix, and is analogous to the scalar multiplicative model (1.2). Lefkovitch (1965) proposed MPMs where subpopulations are distinguished by life stage, e.g., young, immature, and mature, thus a stage-structured model in contrast to an age-structured model. Of course, partitioning by gender, genotype, and many other subpopulation identifiers is possible. This simple structure, $\mathbf{n}_t = \mathbf{L}\mathbf{n}_{t-1}$, has been extended in many ways including time varying $\mathbf{L}$, the use of covariates to model the components of $\mathbf{L}$, adding stochasticity and density dependence.

1.4.1 Analysis of MPMs

Apparently simple MPMs, such as (1.9), can yield complex dynamics depending upon the components of $\mathbf{L}$, and the many extensions of MPMs have added to this complexity. To gain deeper understanding of the dynamics of MPMS, Caswell (2001, p. 18) developed four sets of questions, which have been paraphrased below.

1. *What is the asymptotic behavior of the MPM?* As time increases, does the total population grow or decline exponentially? Do the relative proportions of each subpopulation become constant? Does the

population approach an upper bound (carrying capacity)? Do the total population and individual subpopulation abundances oscillate (in a damped or undamped manner)? Do the abundances display periodicity? Do the abundances become chaotic?

2. *Is the MPM ergodic?* In other words, are the asymptotic dynamics independent of the initial conditions, e.g., independent of the actual values of $\mathbf{n}_0$?
3. *What are the transient dynamics?* What are the dynamics like in the short term as opposed to the asymptotic or limiting results?
4. *How sensitive are the results to the values of the elements of* $\mathbf{L}$*?* The survival probabilities and fecundity rates, for example, are estimates, and will have some degree of estimation error. How much would the population dynamics, including asymptotic and transient dynamics, change if some elements of the matrix were changed "slightly"?

We will not address all these questions further here and refer the interested reader to Caswell (2001). However we will briefly discuss one type of asymptotic behavior, for both deterministic and stochastic MPMs, which is analogous to single population exponential growth models.

1.4.2 Limiting behavior of density independent, time invariate MPMs

Results from matrix algebra can be used to describe the asymptotic behavior of a time invariant projection matrix (see Caswell, 2001, chap 4.5). If the matrix is (a) nonnegative (all elements are ≥ 0), (b) irreducible (e.g., every age class can contribute to every other age class at some point in time), (c) primitive (there is some positive integer k such that every element in the matrix raised to the power k, $\mathbf{L}^k$, is a positive number), then in the limit the population dynamics are either exponential growth or decay, i.e., $A^T\mathbf{n}_t = \lambda\mathbf{n}_t$, where λ is a scalar value that is multiplied against each component of the vector $\mathbf{n}_t$. Further, the relative proportions of each component of $\mathbf{n}_t$ will remain constant.

For example, consider an MPM with three age classes (Young, Adult, Adult) and an initial abundance $\mathbf{n}_0^{'}$ = (100,50,10) and the following Leslie matrix

$$\mathbf{L} = \begin{bmatrix} \gamma_{Young} & \gamma_{Adult} & \gamma_{Old} \\ \phi_{Young} & 0 & 0 \\ 0 & \phi_{Adult} & \phi_{Old} \end{bmatrix} = \begin{bmatrix} 0.0 & 1.2 & 1.4 \\ 0.3 & 0.0 & 0.0 \\ 0.0 & 0.5 & 0.9 \end{bmatrix} \quad (1.10)$$

The population abundances over 9 iterations are:

Stage	1	2	3	4	5	6	7	8	9	10
Young	100	74	84	90	103	116	131	148	167	189
Adult	50	30	22	25	27	31	35	39	44	50
Old	10	34	46	52	59	67	76	86	97	109

The population growth rates, per stage, over time:

Stage	2	3	4	5	6	7	8	9	10
Young	0.74	1.13	1.08	1.14	1.12	1.13	1.13	1.13	1.13
Adult	0.60	0.74	1.13	1.08	1.14	1.12	1.13	1.13	1.13
Old	3.40	1.34	1.14	1.14	1.13	1.13	1.13	1.13	1.13

Thus after six generations the annual growth rate reaches 13% and stays there. The fraction of the population in each stage class stabilizes as well:

Stage	1	2	3	4	5	6	7	8	9	10
Young	0.62	0.54	0.55	0.54	0.54	0.54	0.54	0.54	0.54	0.54
Adult	0.31	0.22	0.15	0.15	0.14	0.14	0.14	0.14	0.14	0.14
Old	0.06	0.25	0.30	0.31	0.31	0.31	0.31	0.31	0.31	0.31

Thus, after six generations the fractions in the Young, Adult, and Old stages remain 0.54, 0.14, and 0.31.

The limiting population growth rate and proportions of each category can be determined analytically using matrix algebra, in particular, by carrying out an eigen analysis of $\mathbf{L}$. For a p by p matrix $\mathbf{L}$, the eigen analysis yields p eigenvalues, $\lambda_1, \ldots, \lambda_p$, and p corresponding right eigenvectors, $\mathbf{v}_1, \ldots, \mathbf{v}_p$. An eigenvalue and its corresponding eigenvector have the relationship, $\mathbf{L}\mathbf{v}_i = \lambda_i \mathbf{v}_i$. Denote the largest eigenvalue λ_1 and its corresponding eigenvector $\mathbf{v}_1$. Then λ_1 is equal to limiting population growth rate, in the example 1.13 (more precisely, 1.12938), and dividing each element of $\mathbf{v_1}$ by its total yields the limiting fractions, here (0.54, 0.14, 0.31).

1.4.3 Stochasticity

One way to add stochasticity to MPMs is to randomly draw elements of the matrix from probability distributions, e.g., randomly draw survival probabilities for age a individuals, thereby introducing environmental stochasticity. Under some conditions, in the absence of density dependence for example, the introduction of environmental, or demographic, stochasticity will not appreciably alter the asymptotic dynamics from that of a deterministic MPM. In other words, the above eigen analysis results more or less hold: in the limit there is an average growth rate and stable population structure. Caswell (2001, Chap. 14) provides details of these results (with some of earliest work

from Cohen, 1976; Tuljapurkar and Orzack, 1980). Below we closely follow (Caswell, 2001, p. 393) and somewhat mimic the derivation of the asymptotic distribution of the stochastic univariate model shown in (1.5 - 1.7). We start with a stochastic process of matrices, $\mathbf{L}_1$, $\mathbf{L}_2$,..., which satisfy certain regularity conditions, including being stationary (the joint distribution for $(\mathbf{L}_{t_1}, \mathbf{L}_{t_2}, \ldots, \mathbf{L}_{t_n})$ is the same as that for $(\mathbf{L}_{t_1+h}, \mathbf{L}_{t_2+h}, \ldots, \mathbf{L}_{t_n+h})$ for any finite $n > 0$, $t_1, t_2, \ldots, t_n$, and $h > 0$), and ergodic (roughly put, the initial value of $\mathbf{L}_1$ does not affect the eventual behavior of the sequence). Further assume an upper bound on the magnitude of the initial matrix, $E(ln^+||\mathbf{L}||_1) < \infty$, where $||\mathbf{L}|| = \sup_{\mathbf{n}\neq 0} \frac{||\mathbf{Ln}||}{||\mathbf{n}||}$ and $\ln^+(x) = \max(0, \ln(x))$. The total population size at time t, denoted $N(t)$, is the vector norm of $\mathbf{n}_t$ ($||\mathbf{n}_t|| = \sum_i |n_{t,i}|$). Given an initial vector $\mathbf{n}_0$:

$$\begin{aligned} N(t) &= ||\mathbf{n}_t|| = \left|\left|\prod_{i=1}^{t} \mathbf{L}_i \mathbf{n}_0\right|\right| && (1.11) \\ &\Rightarrow \\ \frac{1}{t}\ln\left(N(t)\right) &= \frac{1}{t}\ln\left|\left|\prod_{i=1}^{t} \mathbf{L}_i \mathbf{n}_0\right|\right|. && (1.12) \end{aligned}$$

Furstenberg and Kesten (1960) proved that, with probability 1, the limit of (1.12) exists:

$$\lim_{t\to\infty} \frac{1}{t}\ln\left(N(t)\right) = \lim_{t\to\infty} \frac{1}{t}\ln\left|\left|\prod_{i=1}^{t} \mathbf{L}_i \mathbf{n}_0\right|\right| = \ln(\lambda_s), \quad (1.13)$$

where λ_s is called the stochastic growth rate. Lower and upper bounds on λ_s can be calculated from the average minimum row sums and average maximum row sums of the matrices, namely,

$$\sum_i \pi_i R^{(i)}_{\min} \leq \ln(\lambda_s) \leq \sum_i \pi_i R^{(i)}_{\max} \quad (1.14)$$

where π_i is the asymptotic probability of environment i occurring (corresponding to matrix $\mathbf{L}_i$) and $R^{(i)}_{\min}$ and $R^{(i)}_{\max}$ are the minimum and maximum row sums of $\mathbf{L}_i$ (Caswell, 2001, p. 395).

With further conditions on the matrices, $\mathbf{L}_i$, including nonnegativity, the asymptotic distribution of the population total is lognormal:

$$N(t) \sim \text{Asymptotic Lognormal}\left(\exp(t\ln(\lambda_s)), t\sigma^2\right) \quad (1.15)$$

where σ^2 is some constant. Thus, similar to (1.7), the asymptotic median of the population total is the same as for a univariate exponential population growth model, and λ_s is analogous to the largest eigenvalue, λ_1, of a deterministic MPM.

1.4.4 Building block approach to matrix construction

Deterministic skeletons for relatively complex MPMs can be constructed using a building block approach (Buckland et al. (2007); Newman et al. (2014)). A crucial assumption is the approach is that there is a particular sequence to processes which operate on a vector of population abundances, such as survival, then movement, then reproduction. An example from Newman et al. (2014, eq. 2.11, p. 18) has two size-class subpopulations, small and large, and a sequence of three processes: survival, followed by growth (from small to large), and then reproduction. The survival probabilities are size specific (ϕ_S and ϕ_L), the probability that a small individual becomes large is π, and only large individuals can reproduce and they do so with rate ρ.

$$\begin{aligned}\begin{bmatrix} n_{S,t} \\ n_{L,t} \end{bmatrix} &= \begin{bmatrix} 1 & \rho \\ 0 & 1 \end{bmatrix} \begin{bmatrix} 1-\pi & 0 \\ \pi & 1 \end{bmatrix} \begin{bmatrix} \phi_S & 0 \\ 0 & \phi_L \end{bmatrix} \begin{bmatrix} n_{S,t-1} \\ n_{L,t-1} \end{bmatrix} \\ &= \begin{bmatrix} (1-\pi+\rho\pi)\phi_S & \rho\phi_L \\ \pi\phi_L & \phi_L \end{bmatrix} \begin{bmatrix} n_{S,t-1} \\ n_{L,t-1} \end{bmatrix} = \mathbf{L}\mathbf{n}_{t-1} \end{aligned} \tag{1.16}$$

The matrix in (1.16) is an example of a Lefkovitch matrix which is arguably more simply constructed by using such a building block approach than by trying to construct the final matrix in a single operation.

1.4.5 Determining the elements of projection matrices

The most common way to use MPMs has been to plug in estimates of matrix components from various, and often independent, studies, and then make population projections using those point estimates. Caswell (2001, p. 22), for example, states that, to fill the elements of the matrix, life tables are used. Life tables contain mortality probabilities, the probability that an individual of age a will die before reaching age $a+1$, and maternity functions, the expected number of offspring that an age a individual will produce in the next year, from which survival probabilities ϕ and reproductive rates γ (1.9) can be calculated. However, how mortality probabilities and maternity functions are constructed in the first place may be no trivial task. With wildlife populations, mark-recapture studies where animals are aged at time of marking can provide estimates of age-specific survival, and, in some situations, estimates of reproductive success. Of course, the addition of more subpopulations and processes increases the "data requirements and mathematical complexities [which] can quickly overwhelm an investigation of these parameter-rich models" (Williams et al., 2002, p161).

An alternative to the above approach of estimating matrix elements separately from inference about population abundances is to combine stochastic population dynamics with statistical sampling error, or estimation uncertainty, in matrix elements and population abundances. The SSM framework provides a structure for doing this and is discussed in Section 1.7.

1.4.6 Density dependent MPMs

Density dependence can be introduced into MPMs by simply making some of the elements of the projection matrix density dependent. For example, referring to (1.10), the fecundity of the old group could be expressed as a function of the total abundance of adult and old individuals, $\gamma_{Old,t} = (n_{Adult,t} + n_{Old,t}) \exp(-c(n_{Adult,t} + n_{Old,t}))$, a variant of the Ricker model. The linearity aspect of the MPM is subsequently altered and the analyses carried out for density independent MPMs do not directly apply, e.g., the eigen analysis is no longer directly applicable. See Caswell (2001, Chap. 16) for detailed discussion of a variety of density dependent models, subsequent dynamics, and analytical approaches.

1.5 Integral Projection Models, IPMs

The partitioning of a population into discrete subpopulations, namely formulating a structured population, may be arbitrary when natural divisions are lacking. For example, suppose individual weight (in kg) is the feature used to subdivide the population for an MPM. The specified weight classes, small, medium, and large, necessarily have arbitrary boundaries, say, (0,5), [5,10), [10+]. An animal weighing 4.99 kg is labeled small and one weighing 5.0 kg is medium. Those two individuals will be treated differently in terms of population processes, e.g., the survival probability is 0.5 for small individuals and 0.8 for medium individuals, while the actual survival probabilities for both individuals may be much more similar. Integral Projection Models (IPMS; Easterling et al., 2000), sometimes called integrodifference equation models (see Caswell, 2001, for historical references), are a modeling approach that maintains the continuous nature of a factor that distinguishes population members, while (generally) maintaining the discrete time step characteristic of MPMs.

1.5.1 Kernel structure of IPMs.

The core of an IPM is the *kernel*, denoted $K(z\prime_{t+1}|z_t)$, which is analogous to an element in the transition matrix of an MPM. The kernel can be viewed as a conditional probability density function for the "probability" that an animal of size z at time t, denoted z_t, is size $z\prime$ at time $t+1$, denoted $z\prime_{t+1}$. The word probability is put in quotation marks as this is a density not a probability. More accurately $K(z\prime_{t+1}|z_t)\Delta$ is an approximate probability for such a movement from size z_t to a size in an interval of width Δ containing $z\prime_{t+1}$, e.g., $z\prime_{t+1} \pm 0.5\Delta$. The number of individuals in a given size class at time $t+1$ is then the sum of all individuals of *any* size class at time t, $n(z_t^*)$,

that survive, grow, and/or contribute to individuals of size class z_{t+1} at time $t+1$ where $z_t^* \in \Omega$ and Ω is a suitably large range of sizes, so

$$n(z\prime_{t+1}) \quad = \quad \int_{z_t \in \Omega} K(z\prime_{t+1}|z_t) n(z_t) dz_t \tag{1.17}$$

A simpler version of the kernel is time invariant, $F(z\prime|z)$, where the conditional density for the contribution to size class $z\prime$ at time $t+1$ from size class z_t is the same for all times t.

The population growth process is the result of multiple processes, including survival and reproduction. So the kernel K can be decomposed into survival of the current population and reproduction entering the population. Here, however, individual size is also a factor and survival and reproduction is into a specific size class, z_{t+1}. Thus growth from size class z_t to z_{t+1} is a third process to account for. The resulting partitioning of the kernel is

$$K(z\prime_{t+1}|z_t) \quad = \quad P(z\prime_{t+1}|z_t) + F(z\prime_{t+1}|z_t) \tag{1.18}$$

where P is the survival/growth kernel, the combined conditional density for surviving to time $t+1$ and changing to size class z_{t+1}, and F is the fecundity kernel, the conditional density for recruits at time $t+1$ of size z_{t+1} (Merow et al., 2014).

There are a wide variety of formulations for the survival/growth kernel. One formulation is to treat the two processes as independent, the result being the product of the conditional probability of surviving, $\phi(z_t)$, and the conditional density of moving to size class $z\prime$, $g(z\prime_{t+1}|z_t)$:

$$P(z\prime_{t+1}|z_t) \quad = \quad \phi(z_t) g(z\prime_{t+1}|z_t) \tag{1.19}$$

In principle, a joint density for survival and growth could be used; e.g., movement to a much larger size class is linked with lowered survival probability. The survival probability could be a more complicated function of competing or sequential mortality factors; e.g., there are two mortality processes occurring in sequence, $\phi(z_t) = \phi_{1,z_t} \phi_{2,z_t}$.

The fecundity kernel can be made complex as well. For example, it could be a function of four processes: a size dependent probability distribution for the number of eggs produced, $f(E|z_t)$, a probability that the eggs are fertilized, p_E, a probability that the fertilized eggs will hatch, p_h, and a density function for the size of hatched larvae, $h(z\prime)$. Then

$$F(z\prime_{t+1}|z_t) \quad = \quad f(E|z_t) p_E p_h h(z\prime) \tag{1.20}$$

Merow et al. (2014) note that a common feature of the survival/growth and fecundity kernel formulations is an *individual component*, e.g., $\phi(z_t)$ in (1.19) and $(f(E|z_t)p_E p_h)$ in (1.20), and a *size redistribution component*, e.g., $g(z\prime_{t+1}|z_t)$ in (1.19) and $h(z\prime)$ in (1.20).

1.5.2 Implementation of an IPM

Equation (1.17) is analogous to the generation of a single component in the state vector of an MPM. With an MPM, the entire state vector at time $t+1$ is $\mathbf{n}_{t+1} = L\mathbf{n}_t$, where the ith entry in $\mathbf{n}_{t+1}$, denoted $n_{i,t+1}$, is the following sum:

$$n_{i,t+1} \quad = \quad \sum_{j=1}^{p} L_{i,j} n_{j,t} \tag{1.21}$$

where L has p columns. Each $L_{i,j}$ in the summation is akin to a kernel function as it is the per individual contribution from "size" class i at time t to "size" class j from time $t+1$. If the vector $\mathbf{n}_t$ is further partitioned into a relative large number of size classes, the summation operation in (1.21) approaches an integration operation.

Implementation of an IPM is in practice the reverse operation. Referring to the integral in (1.17), the interval Ω, which contains the range of size classes that can contribute to size class $z\prime$, is partitioned into m size classes. A finite sum approximation to integration, e.g., the midpoint rule, the trapezoid rule, or Simpson's rule, is used calculate the number of individuals in size class $z\prime$. An example of the midpoint rule: suppose Ω is an interval $[L, U]$ which is partitioned into m intervals of equal length $(U-L)/h$, and let z_i be the midpoint of the ith size class, also known as mesh points (Rees et al., 2014), where

$$z_i \quad = \quad L + (i - 0.5) * j, \quad i = 1, 2, \ldots, m$$

The integral (1.17) can be approximated by

$$n(z\prime_{t+1}) \quad \approx \quad \sum_{i=1}^{m} K(z\prime|z_i) h n(z_{i,t}) \tag{1.22}$$

1.5.3 Estimation of kernel components

The problem of specifying kernel components parallels the problem of determining components of the transition matrices in MPMs. Assuming that relevant data on size, survival, reproduction success, etc, are available, there are many standard statistical model fitting procedures, linear regression, nonlinear regression, generalized linear models including logistic regression, and generalized additive models, that can be used to construct the components of $K(z\prime_{t+1}|z_t)$. Likewise, many of the associated model fit diagnostic procedures could, and should be, used to assess the quality of the estimated components of the kernel (Rees et al., 2014).

A number of probability and density functions are needed to calculate the transition densities of the survival/growth kernel (e.g., (1.19), and the fecundity kernel (e.g., (1.20)). For individual components that are probabilities,

e.g., the conditional probability of survival, sample data on size conditional outcomes can be used to calculate estimates. For example, a mark-recovery study of banded ducks could provide size-specific annual survival probabilities based on a smooth fitted survival function, e.g., $\log(\phi/(1-\phi))\,|z = \beta_0 + \beta_1 z$. Whether or not time-specific functions could be fit may depend upon the number of years of data available. Survival probabilities can be a function of size and environmental covariates, e.g., winter temperatures. For size redistribution components, such as the conditional density for moving from size class z to z^* in (1.19), size measurements made over time on multiple individuals are required.

Inference methods for IPMs are continually developing. For example, Ghosh et al. (2012) use Bayesian hierarchical models where the size distribution is a point pattern on some interval and carry out an integrated analysis that combines the parameter estimation/model fitting stage and the projection stage.

1.5.4 Application, use and analysis of IPMs

Plant species were the most common organisms in early applications of IPMs, e.g., Northern Monkhood (Easterling et al., 2000), with growth transitions between different plant sizes, e.g., stem diameter, and processes like flowering strategies. The scope of applications has since expanded to include birds (Great tits, Childs et al., 2016), arachnids (soil mites, Brooks et al., 2015), mammals (Soay sheep), diseases (hosts and parasites, Metcalf et al., 2016).

The questions asked of MPMs in Section 1.4.1 can be asked of IPMs. Is there a limiting population growth rate, a dominant eigenvalue λ_1 and corresponding stable "size" class distribution? Ellner and Rees (2006) gives examples of sensitivity analyses of IPMs. Software for IPMs includes the R package `IPMpack`.

In addition to analysis of population dynamics, ecological inference using IPMs includes analysis of evolutionary strategies (Ellner and Rees, 2006). Brooks et al. (2015) separated out the effects of individual body size on developmental rates from the effects of environmental conditions on reproductive rates. Metcalf et al. (2016) examined the feedback between host and parasite in an epidemiological analysis.

1.6 Individual Based Models, IBMs

Individual based models in ecology (IBMs; DeAngelis and Grimm, 2013) are computer simulation procedures that can track the entire life history of multiple individuals simultaneously. Variables tracked include emergence into the population (date of birth, germination, hatch date), size at birth, sex, size

over time, time and duration of sexual maturity and reproduction, spatial location and movement, senescence, and death. A central feature is the modeling of interactions of individuals with each other, including individuals of the same species, e.g., reflecting competition for resources and density dependence, and individuals of different species, e.g., reflecting predator-prey dynamics or, more broadly, ecological community interactions. Another key feature is the simulation of interactions of individuals with their abiotic environment, e.g., air temperature and precipitation, and their biotic environment excluding like individuals, e.g., vegetative browse and zooplankton.

The opportunity to insert complexity into dynamic processes underlying demographics is relatively unlimited, constrained primarily by computer storage and processing speed. Population level properties can be examined at any time in the simulation process by aggregating the states of individuals in arbitrary ways. For example, a simulation starts at time t_0 with a vector of 1000 individuals where each individual has an associated vector of initial conditions such as age, weight, sex, spatial location, and maturity. Survival, growth, movement, and reproduction processes are then applied to each individual and, at time t_1, numbers of individuals in different spatial regions further distinguished by sex and age class, say, are tallied to yield abundances of multiple subpopulations. Repeating the simulation and aggregation K times yields a multivariate time series of subpopulation abundances, $\mathbf{n_{t_1}}$, $\mathbf{n_{t_2}}$, ..., $\mathbf{n}_{t_K}$. Analysis of population level dynamics can then be conducted, studying such things as the effects of region-specific harvest regulations on different sub-populations of deer, for example. If the effects of environmental and anthropogenic factors on the population dynamics cannot be readily examined analytically, IBM output can provide some experiential, albeit simulated, insight.

1.6.1 Statistical designs for and analysis of IBMs

The simulation nature of IBMs with multiple attributes and multiple levels to attributes lends itself to using methods from the statistical design of experiments to construct a time series of any length with an arbitrary number of sub-populations. For example, if the attributes of interest are sex, spatial location, and age class with corresponding levels of (female, male), (I, II, III, IV) regions, and ages (0,1,2,3+), then a factorial design with $2\times4\times4 = 32$ "treatment" combinations can be conducted with r replications of each combination. Statistical methods such as analysis of variance or response surface modeling can then be used to examine the effects of the factors and treatment combinations. Aggregated data can be used to construct simple MPMs, like year-specific Leslie matrices, and methods for assessing MPMs, such as calculating annual finite population growth rates for multiple years can be employed (for such an example, see Rose et al., 2013).

The computational burden of IBMs can grow in a number of ways. First, as the number of attributes of interest and the levels of each attribute in-

creases, the number of treatment combinations can grow rapidly. Second, as the level of environmental stochasticity (or demographic) increases, the number of replicates required to provide a desired level of precision for estimates of average population level responses increases as well. Third, questions about the effects of the distribution of initial attribute values at time t_0 as well as questions about the nature of the processes, e.g., density dependent or density independent recruitment success or the chosen value, or distribution of values, for juvenile survival probabilities, can lead to extensive sensitivity analyses.

1.6.2 Comparison with population models

In contrast to population models, such as the Ricker model (1.8), for which long term population dynamics such as exponential growth, an asymptotic upper bound, or periodicity can sometimes be determined analytically or by elementary computer simulation, population-level behavior for IBMs is an *emergent* property. The dynamics are the result of potentially complex interactions of individuals with each other and with their abiotic environment (DeAngelis and Grimm, 2013), and can demonstrate "the importance of local interactions between individuals in ecological systems" (Judson, 1994).

A succinct way to contrast population-level models and IBMs is top-down versus bottom-up. Population-level models are *top-down* in that they predict what happens to individuals as function of population level characteristics, e.g., fecundity of the individual decreases as the total population abundance increases (density dependence exists). Conversely, IBMs are *bottom-up* in that modeling begins with the characteristics of multiple individuals and manifests characteristics of the population as a whole. An interesting example of the latter is with *Anolis* lizards in the Caribbean (discussed in Roughgarden, 2012) where an IBM simulated energy gained per unit time after a lizard consumed a prey item as a function of distance from the prey and the optimal foraging distance could then be determined. From that model for the "energy capture" the daily growth rate of the lizard was predicted, with distinction made between growth prior to reproductive stage and during the reproductive stage. Using these results an optimal growth rate, as a function of age, was calculated, which was then used with information on survival probabilities and maternity rates to determine that optimal female body size was 45mm. As Roughgarden (2012) said "[t]his example illustrates a complete and successful modeling protocol that begins with the properties of an individual and culminates in the an evolutionary prediction of the adult body size for lizards on an island in the absence of congeneric competitors".

1.6.3 Applications of IBMs

The earliest applications of IBMs in ecology were mostly in forestry, and such applications remain common. In the IBM JABOWA (Botkin et al., 1972), individual trees were the fundamental entities and the central measure on each

tree was its stem diameter (at some height on the tree). Other tree measures such as volume and crown biomass can be functions of diameter. Emergence, growth, and death of a tree are functions of interactions with neighboring trees, their size and proximity and the degree to which they compete for resources like light and water, for example, and functions of interactions with the abiotic environment, e.g., soil type and chemistry, precipitation, temperature, and light. Forestry IBMs have been used for management purposes, e.g., to predict growth and yield of commercially harvested species, as well as purely scientific reasons, i.e., to "explore ecological mechanisms and patterns of structure and functional dynamics in natural forest ecosystem" (Liu and Ashton, 1995).

Applications to fish populations are common as well, where IBMs "track the attributes of individual fish through time and aggregate them to generate insights into population function" (Van Winkle et al., 1993). IBMs simulate how fish of different phenotypes interact with their biotic and abiotic environment. Differences in phenotype can refer to differences in length, weight, sex, and age, the biotic environment can include prey items, such as zooplankton or vegetation, and the abiotic environment can include water temperature, salinity, water clarity. An IBM for a small estuarine fish, delta smelt (*Hypomesus transpacificus*, Rose et al., 2013) also included bioenergetics considerations, namely the transformation of consumed prey into fish growth.

IBMs in ecology can be broadly divided into applications for (individual) populations, communities and ecosystems. Single population-level IBMs have been mentioned above, e.g., *Anolis* lizards and Delta Smelt, but IBMs have used to model predator-prey dynamics (Cuddington and Yodzis, 2002). A community-level application by Weiss et al. (2014) used an IBM to simulate how the dynamics of a community assembly of 90 hypothetical plant types were affected by soil attributes and grazing intensities. The results were then compared to field-based observations of species richness and diversity. Least common are ecosystems level applications; a hypothetical food web system used an IBM to model interactions between three trophic levels, plant, herbivore and carnivore (Schmitz and Booth, 1997).

1.6.4 Data needs and structure

IBMs have at least three levels of data needs. One is an initial individual attribute vector (Van Winkle et al., 1993), and initial values for components of the biotic and abiotic environment. When proximity to other individuals is a factor in the dynamics, an initial spatial distribution is needed and locations might be randomly placed as in a Poisson process, systematically placed, clustered, or placed with probabilities proportional to particular habitat conditions. Other individual attributes, e.g., size, sex, age, need to be assigned. To achieve greater realism, the actual multivariate distribution of such attributes should be mimicked. Initial biotic attributes can include type, abundance, and spatial location of competitors, predators, and food items. Initial abiotic fea-

tures may be relatively static, e.g., soil types, water sources, or dynamic, e.g., air temperature and precipitation.

A second data need is for information about how the individuals interact with each other and with their environment. For example, how is the probability of survival affected by the availability and proximity to food items? How is movement affected by population density, biotic and abiotic features?

A third data need is field-based observations to verify that IBM output, and apparent emergent population level properties, e.g., collective survival, reproduction, and movement rates, are reasonable.

Given these data needs, IBMs, particularly those designed for specific applied problems have been criticized as being too "data hungry" (Grimm and Railsback, 2013). Available data may thus constrain and guide IBM formulation, affecting things like the time step resolution, spatial scope, number of attributes followed, and number of interactive processes simulated.

1.6.5 Relationship with IPMs

Longitudinal data on individuals are central to both IPMs and IBMs. IPMs *use* such data to model population, or sub-population, level probabilities of transitions from one attribute value to another. In contrast, IBMs, starting at time $t = 0$ with a vector of n_0 individuals each with an associated attribute vector, *generate* longitudinal data per individual. Such data generated by IBMs can be used to evaluate fitting procedures for IPMs and the subsequent performance of IPMs can be evaluated by comparing IPM predictions to the "true" values generated by simulated IBM output (Rees et al., 2014).

1.7 State-Space Models, SSMs

State-space models (SSMs) are models for two parallel time series, a state process and an observation time series. The state process time series describes the temporal evolution of the true, but generally unknown, state of nature; it is here denoted $\mathbf{n}_t$, t=0, 1, 2, ..., T, where $\mathbf{n}_t$ can be a vector of varying length. The state $\mathbf{n}_0$ is referred to as the initial state. The observation time series, denoted $\mathbf{y}_t$ with t=1,2,..., T, is a sequence of imperfect or inexact measurements of the state process time series. The integer valued subscripting of both time series is used here, $t_1, t_2, \ldots, t_T$, but arbitrary time points are possible. The time series indexing for both time series do not necessarily coincide, e.g., there could be half the observations if the state is only observed every other time point, although statistical estimation limitations might occur. Also, the dimensions of $\mathbf{n}_t$ and $\mathbf{y}_t$ need not be the same, although situations where the dimensions differ can affect estimability. For an ecological example: $\mathbf{n}_t$ is a

vector of true abundances of subpopulations at time t and the components of $\mathbf{y}_t$ are estimates of one or more components of $\mathbf{n}_t$.

The probabilistic structure of a SSM is a paired sequence of probability distributions (probability mass functions for integer valued components or probability density functions for continuous valued components) that characterize the evolution of $\mathbf{n}_t$ and the relationship between $\mathbf{y}_t$ and $\mathbf{n}_t$. The the probability distribution for $\mathbf{n}_t$ is typically first order Markov, i.e., $\mathbf{n}_t$ given $\mathbf{n}_{t-1}$ is conditionally independent of all other states, and $\mathbf{y}_t$ given $\mathbf{n}_t$ is independent of all other state vectors and all other observation vectors.

1.7.1 Normal dynamic linear models

A classic SSM, originating from Kalman (1960), is the normal dynamic linear model (NDLM); for example,

$$\begin{aligned} \mathbf{n}_0 &\sim D(\theta) \\ \mathbf{n}_t|\mathbf{n}_{t-1} &\sim \text{MVN}\left(\mathbf{L}\mathbf{n}_{t-1}, \Sigma\right), \quad t = 1, 2, \ldots, T \\ \mathbf{y}_t|\mathbf{n}_t &\sim \text{MVN}\left(\mathbf{B}\mathbf{n}_t, \Omega\right), \quad t = 1, 2, \ldots, T \end{aligned}$$

where $D(\theta)$ denotes an arbitrary probability distribution with parameter θ which may be degenerate, i.e., $\mathbf{n}_0$ is a fixed value, MVN is multivariate normal, L and B are matrices, and Σ and Ω are variance-covariance matrices. As denoted here all the matrices are time invariant, but that is not necessary. Given $\mathbf{y}_t$, t=1,2,..., T, and the values of $\mathbf{n}_0$, $\mathbf{L}$, $\mathbf{B}$, Σ, and Ω, the conditional distribution of $\mathbf{n}_t$, which is multivariate normal, can be determined using an algorithm known as the Kalman filter. The Kalman filter also yields the calculated value of the likelihood (the joint marginal distribution of $\mathbf{y}_t$, t=1,2,...,T), which can then, in principle, be used to estimate unknown parameters of the transition and variance-covariance matrices. However, in practice there are considerable restrictions on the estimability of the parameters, and potentially high correlations between estimates of Σ and Ω (Dennis et al., 2006). The notation $\mathbf{L}$ for the state transition matrix was selected to suggest the notion of a Leslie matrix (1.9) as SSM extensions of MPMs are not uncommon (Sullivan (1992); Newman (1998), and see the gray whale example in section 6.4.2.2 of Newman et al. (2014)).

1.7.2 Non-normal, nonlinear SSMs

The NDLM structure is often too constricting and unrealistic for population dynamics modeling. More realistic state-space models can on occasion be "shoe-horned" into the NDLM framework by a mathematical transformation of states or observations, e.g., a log transformation, and thus allow usage of the Kalman filter. For example, Dennis et al. (2006) used a stochastic Gompertz model for the state process distribution.

$$n_t|n_{t-1} = \lambda n_{t-1}^{1+\alpha} \exp \epsilon_t$$

where $\alpha \leq 0$ and $\epsilon_t \sim \text{Normal}(0,\sigma_\epsilon^2)$. A natural log transform yields a linear normal state distribution.

$$\ln(n_t)|\ln(n_{t-1}) \quad \sim \quad \text{Normal}\left(\ln(\lambda) + (1+\alpha)\ln(n_{t-1}), \sigma_\epsilon^2\right)$$

Another way to modify an otherwise non-normal, and perhaps nonlinear SSM, into a NDLM approximation is to work with just the first two moments of the state process distribution and then use the mean and covariance structure as the normal mean vector and covariance matrix. Newman (1998) and Newman et al. (2014) give examples of such substitutions. A simplistic univariate example is to suppose that a scalar valued state n_t is Binomial(n_{t-1}, ϕ_t), where ϕ_t is the survival probability, perhaps a function of covariates. The conditional expected value of n_t is of course $\phi_t n_{t-1} \equiv L_t n_{t-1}$, and the conditional variance is $n_{t-1}\phi_t(1-\phi_t) \equiv Q_t$. Other, perhaps somewhat slight, departures from the NDLM formulation can be accommodated by Taylor series transformations of the process, using the Extended Kalman Filter (EKF; Einicke and White, 1999). A more recent alternative to the EKF, which has been shown to have at least equal and often far superior performance (Durbin and Koopman, 2012, p. 236) is the Unscented Kalman Filter (Julier and Uhlmann, 2004).

Computer intensive Monte Carlo methods such as Markov chain Monte Carlo (MCMC, Gilks et al., 1996) and Sequential Monte Carlo (SMC Doucet and Gordon, 2001) offer the ultimate flexibility for fitting nonlinear, non-normal SSMs. With the MC procedures applied to such SSMs, Bayesian inference has been the dominant approach, but not always (see De Valpine, 2003; Ionides et al., 2006, for exceptions). One of the first ecological applications using MC methods was by Meyer and Millar (1999), who used the program BUGS (Bayesian inference Using Gibbs Sampling) to fit an SSM with scalar states and observations. The state was scaled biomass ($p_t = B_t/K$), rather than abundance, where biomass (B_t) was divided by carrying capacity, K, thus $0 < p_t \leq 1$), and the observation was a biased measure of scaled biomass, an index (y_t):

$$\begin{aligned} p_t|p_{t-1} \quad &\sim \quad \text{Lognormal}\left(\ln\left(p_{t-1} + r p_{t-1}(1-p_t) - \frac{c_{t-1}}{K}\right), \sigma_p^2\right) \\ y_t|p_t \quad &\sim \quad \text{Lognormal}\left(\ln\left(qKp_t\right), \sigma_o^2\right) \end{aligned}$$

Thus the SSM was intrinsically nonlinear (no transformation of the state would linearize the mean structure) and non-normal.

1.7.3 Hierarchical and continuous time SSMs

An extension of SSMs is a hierarchical state-space model (HSSM). A general formulation for an HSSM in a Bayesian framework is the following

$$\begin{aligned} \text{Prior distribution} &: \pi(\eta, \omega) && (1.23)\\ \text{Stochastic variation in parameter} &: h(\Theta_t, \eta) && (1.24)\\ \text{State process model} &: g_t(\mathbf{n}_t|\mathbf{n}_{t-1}, \Theta_t) && (1.25)\\ \text{Observation model} &: f_t(\mathbf{y}_t|\mathbf{n}_t, \Omega) && (1.26) \end{aligned}$$

where π, h, g_t, and f_t denote probability distribution functions. Newman and Lindley (2006) used Sequential Monte Carlo to fit a Bayesian HSSM to salmon data which included both environmental and demographic stochasticity. The environmental stochasticity was modeled as above with separate distributions for year-specific survival and maturation probabilities. Demographic stochasticity was incorporated in the state process equations using multinomial distributions to reflect between individual variation in survival and maturation (although given the population size, the influence of demographic stochasticity on the results was likely minimal).

Durbin and Koopman (2012) discuss continuous time SSMs for a couple cases including what is called a continuous time local level SSM. Here $n(t) = n(0) + \sigma_\epsilon\ \omega(t)$, where ω_t arises from a Brownian motion process, which means $\omega(0)$=0, $\omega(t) \sim$ Normal(0,t) for $0 < t < \infty$, and "jumps" or increments without common endpoints are independent, e.g., $\omega(2)-\omega(1)$ is independent of $\omega(4)-\omega(3)$. For an ecological application of continuous time SSMs see Johnson et al. (2008) who model the location of marine mammals using telemetry data.

1.8 Concluding Remarks

1.8.1 Omissions and sparse coverage

Continuous time demographic models have been largely ignored here, excepting the Lotka-Volterra predator-prey model. Williams et al. (2002) provides an introduction to continuous Markov processes, including birth and death processes, and Brownian motion in the context of models for animal populations. Differences in the ecological dynamics of discrete time and continuous time models are examined by Gurney and Nisbet (1998). Durbin and Koopman (2012) and Johnson et al. (2008) are references for continuous time SSMs.

Some aspects of ecological theory which have demographic implications that were omitted include fitness, adaptation, and mutation. Effective population size, N_e, of an existing population, here defined as the minimum number of individuals necessary in a hypothetical population that would represent existing populations ability to retain the genetic diversity present, is an im-

portant concept for endangered species, and methods for calculating N_e were not addressed. Coverage of the demography of multiple populations, communities, and ecosystems was scanty, and measures of community structure such as species richness and models for changes in such measures were not mentioned at all. Demographic modeling of ecosystems has been popular in fisheries (Christensen and Pauly, 1992; Walters et al., 1997, 1999) with `Ecopath with Ecosim` and `Ecospace` the leading software.

1.8.2 Recommended literature

For MPMs, Caswell (2001) remains an outstanding reference with near encyclopedic coverage of material to 2001. For stochastic MPMs, the Tuljapurkar (1990) book is a classic.

For IPMs, there are two "How To" papers, Rees et al. (2014) and Merow et al. (2014) which provide the basic components of IPMs, ways of estimating the kernel components, and ways of making the projections (using numerical integration methods). The original paper (Easterling et al., 2000) includes detailed discussion of the advantages of IPMs over MPMs, while Ellner and Rees (2006) include detailed examples of stable population analyses often done with MPMs. More sophisticated and integrated IPM fitting and projection approaches are described by Ghosh et al. (2012).

For IBMs, Grimm and Railsback (2013) provide a book length treatment, with DeAngelis and Grimm (2013) a more recent overview paper. Roughgarden (2012) gives an alternative perspective on the definition of and uses of IBMs, viewing agent-based models as a special case, for example.

For SSMs, Durbin and Koopman (2012) is an extremely thorough book length treatment of SSMs. Two thirds of the book covers linear SSMs, including classical treatment with the Kalman algorithms and extensions. The remainder discusses nonlinear, non-normal SSMs including special cases and quite general formulations that are typically fit by Monte Carlo procedures. Specific focus on the use of SSMs for population dynamics modeling is given by Newman et al. (2014).

1.8.3 Speculations on future developments

Data.

The volume and complexity of data on individual organisms continues to grow as the life spans of biological monitoring programs extend, as new monitoring programs are established, and as data collection technology advances. Electronic monitoring devices, e.g., radio tag collars, acoustic tags, tags that record the diving depths of marine animals, provide increasingly fine temporal and spatial resolution information on individual animal movement. Chemical analyses of organisms yield more information about individual life histories, e.g., chemical analyses of bony structures in fish, such as otoliths, can pinpoint

birth place and migration paths (Secor et al., 1995). Environmental DNA (eDNA) is an emerging tool for indirectly detecting species presence (Thomsen and Willerslev, 2015). Remote sensing is adding increasingly detailed data abiotic environments. In short, "attribute vectors" (Van Winkle et al., 1993) for individuals, populations, and abiotic and biotic environments are getting longer and longer.

Model formulations.

Appreciation of the need to separately model process variation (environmental and demographic stochasticity) and observation noise (e.g., sampling errors) will increase. Consequently, formulation of SSMs, and, more generally, hierarchical models (Kery and Royle, 2016; King et al., 2009), for demographic data will increase. Extensions of MPMs, IPMs, and IBMs that explicitly distinguish both types of variation will likely become more common, too.

Hierarchical extensions of MPMs within the normal dynamic linear model framework of SSMs date back to the 1990s, e.g., Sullivan (1992) and Newman (1998). More recently, Newman et al. (2014), in an application to the Eastern North Pacific gray whales (*Eschrichtius robustus*) population, contrasted an MPM with observation error only with a NDLM extension. Differences in some of the parameter estimates were considerable, e.g., juvenile survival probability was estimated to be 0.9999 (upper bound) for the observation error only model and 0.8281 for the SSM. Advances in model fitting procedures lessen the need to restrict process models to linear formulations, implicit to MPMs, with additive normal (or multiplicative lognormal) distributions. More biologically realistic nonlinear, and non-Gaussian formulations may make applications in the MPM framework less common. However, the MPM structure will remain valuable for formulating approximate deterministic skeletons underlying more realistic models (Buckland et al., 2007).

For IPMs and IBMs, process and observation uncertainty can be readily partitioned and accounted for by computer simulation. With IPMs, bootstrapping the kernel density components yields measures of parameter estimate uncertainty as well as between animal variation. For example, uncertainty about parameters of the growth density model, $g(z\prime_{t+1}|z_t)$, in the survival/growth kernel (1.19), can be assessed by resampling the longitudinal data on sizes to generate a bootstrapped distribution of growth densities. For a given fitted growth density model, simulated variation of individual sizes around the expected size at time $t+1$ reflects demographic variation. For IBMs, computer simulation of between individual variation and parameter uncertainty can be carried out within a designed experiment structure to (a) determine the relative import of specific factors on the model predictions and (b) quantify the degree of uncertainty in model predictions.

Model fitting.

Extended attribute vectors for increasingly large numbers of individuals, along with increasingly complex demographic model formulations, necessitate increasingly complex model fitting procedures. The pace of development for fitting such models is rapid and the variety of model fitting options available is increasing. Here we focus on options for fitting dynamic hierarchical demographic models.

Mathematical integration and numerical optimization are at the heart of hierarchical model fitting procedures, with the integration being over the unobserved state process. In special cases, algorithms exist for analytic evaluation of the integrals, e.g., NDLMs and the Kalman filter. As discussed in section 1.7.2, numerical approximations to nonlinear, but Gaussian, population dynamics models yield models amenable to such analytic solutions. For general hierarchical dynamic models approximate analytic solutions to the integration problems include the Laplace approximation (Tierney and Kadane, 1986) and the Integrated Nested Laplace Approximation (INLA, Rue et al., 2009). The software packages, AD Model Builder (ADMB, Fournier et al., 2012) and Template Model Builder (`https://github.com/kaskr/adcomp/`), use Laplace approximations to integrate over the state process to yield the likelihood and then automatic differentiation for calculating maximum likelihood estimates of the parameters. Widely used and well established software for carrying out the integration using Monte Carlo procedures such as MCMC and sequential Monte Carlo (section 1.7.2 includes WinBUGS (Lunn et al., 2000) and JAGS (Plummer et al., 2003). Two recent software additions are NIMBLE (de Valpine et al., 2015) and the R package `pomp`, both of which allow users to choose from a variety of computer intensive model fitting procedures. NIMBLE extends the BUGS software and allows estimation within Bayesian or likelihood frameworks. The `R` package `pomp`, for "partially observed Markov processes" , contains a variety of procedures for fitting state-space models, with including "sequential Monte Carlo, iterated filtering, particle Markov chain Monte Carlo, approximate Bayesian computation, maximum synthetic likelihood estimation, nonlinear forecasting, and trajectory matching" (King et al., 2016).

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